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Effect of Salinity on Ionic Shifts in Mesohaline Scyphomedusae, *Chrysaora quinquecirrha*

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Abstract. Mesohaline populations of the scyphomedusae *Chrysaora quinquecirrha* are found in salinities ranging from 5‰ to 25‰. Osmotic and ionic adjustments within this salinity range were investigated using *C. quinquecirrha* ephyrae budded from polyps in the laboratory and young medusae collected from the mid-salinity region of the Patuxent River, Maryland. When medusae were transferred from 20‰ salinity to lower salinities (8‰, 12‰), concentrations of sodium and magnesium in tissue and mesogleal fluid fell rapidly and approached those of dilute seawater within 6 hours. There was some recovery of these levels relative to the 8‰ medium, and they were significantly higher than the dilute seawater concentration after 1 week. Tissue concentrations of calcium showed no evidence of being regulated, whereas potassium was strongly regulated such that levels did not fall significantly following transfer of medusae to lower salinities. However, after 1 week, the concentration of potassium in mesogleal fluid approached that of the dilute medium. Extracellular space measured by direct blotting and weighing or using ^{35}S was about 40%. As a result, estimates for intracellular potassium were revised to 17 $mM\ l^{-1}$. The concentration of potassium in tissue remained stable following transfer to lower salinity, despite a substantial osmotic influx of water. This influx was measured as a >20% gain in body weight over 24 h following transfer of medusae from 16‰ to 8‰. Mesogleal fluid was slightly hypo-osmolar to the medium at 15% and 20‰ and slightly hyperosmolar to the medium at 5‰ and 12‰. Sulfate concentrations in mesogleal fluid were 66%–70% those of the external medium. Medusae died or were unable to achieve positive buoyancy at 5‰, which is probably very close to a lower salinity limit for *C. quinquecirrha* in the mesohaline Chesapeake Bay.

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Introduction

Most members of the phylum Cnidaria are marine. Only a few hydrozoans (*e.g., Craspedacusta*) live in fresh water. Some cnidarians occur in low-salinity waters, but species diversity decreases sharply with decreased salinity (Dumont, 1994). In Chesapeake Bay, medusae of the scyphozoan *Chrysaora quinquecirrha* are unusual in tolerating salinities as low as 5‰; the scyphistomae (polyps) are not found where salinities are less than 7‰ and thrive at 10‰ to 25‰ (Cargo and Schultz, 1966, 1967). Purcell (unpubl. data) has determined that asexual reproduction in *C. quinquecirrha* in the mesohaline Chesapeake Bay is limited by both low (<5‰) and high (>25‰) salinities. Differences in reproduction at different salinities may result in part from the physiological cost of salinity adjustment; *i.e.*, energy required for volume regulation may detract from that available for reproductive effort.

Mills (1984) found that a variety of marine hydromedusae and ctenophores adjusted osmotically within a few hours to abrupt changes in salinity between 23‰ and 38‰. Most species tested were able to osmoconform to this salinity range. However, salinity of 19‰ was usually lethal to animals normally found at a salinity of 30%. In experiments using Percoll to change the density but not the tonicity of seawater, medusae made no buoyancy adjustments. Therefore, Mills (1984) concluded that the process was passive osmotic accommodation to the salinity changes, not active density regulation. Studies such as those of Schick (1973) have suggested that amino acids play an important role in maintaining cellular volume

in osmotically stressed cnidarians. In freshwater forms, however, sodium and potassium extrusion followed by water loss from cells (Benos and Prusch, 1972) seems to provide the principal means of regulating cellular volume. Webb *et al.* (1972) examined free amino acids (FAA) in scyphistomae of three species of scyphomedusae, including *C. quinquecirrha.* They found that although FAA concentrations increased linearly with increasing salinity, they were only 0.9% to 4.6% of the total osmotically active substances in the scyphistoma and could not account for its osmotic balance. In summary, there is evidence for both active and passive osmotic processes in pelagic cnidarians.

Little work has been done on ionic regulation in pelagic cnidarians. Robertson (1949) summarized some earlier work on *Aurelia aurita* medusae, showing that the ionic composition of the medusae was not the same as that of the surrounding water and thus suggesting that the medusae can actively control their ionic composition. The finding that sulfate ions were particularly low stimulated interest in the exclusion of heavy ions, specifically sulfate, as a mechanism of buoyancy control in gelatinous zooplankton (Denton and Shaw, 1962; Mackay, 1969; Bidigare and Biggs, 1980; Mills and Vogt, 1984). Mackay (1969) described a saturable, probably active, sulfate transport mechanism with K_m values of 17 to 22 mM l^{-1} in two species of hydromedusae. Bidigare and Biggs (1980) determined that active sulfate loss from the ctenophore *Beroe cucumis* could be compensated by isosmotic chloride exchange. The current research investigated changes in tissue and mesoglea osmolality and cation levels in *C. quinquecirrha* medusae at different salinities. Results were considered in light of salinity-related changes in body size and extracellular space determined either directly or using sulfate.

Materials and Methods

Medusae between 1 and 2 g wet weight (25–30 mm bell diameter) were obtained from the Patuxent River, Maryland, and acclimated in 40-l aquaria containing 16‰ Patuxent River water for 1 wk before experiments. Medusae were fed *Artemia salina* nauplii during the acclimation periods, but they were not fed during experimental treatments unless otherwise stated. Ephyrae were budded from scyphistomae at 20‰ in the laboratory.

Cation measurements

Medusae were netted out of holding tanks, blotted dry in a standardized manner using laboratory wipes, and weighed by introducing them to tared individual polyethylene beakers containing 400 ml of experimental medium. In the two experiments reported here, medusae were transferred from 20‰ to 8‰ and 12‰ at time = 0 h. Six animals were prepared for immediate analysis, and six animals from each treatment were sampled at 6 h, 24 h, and 7 d. Animals were lifted from beakers with large plastic forceps, blotted dry on laboratory wipes, and weighed in plastic weighing dishes. The bell and tentacles were then separated, and the mesoglea was allowed to drain into the weighing dish. A 50-μl sample of mesogleal fluid was pulled into a hematocrit tube and then expelled into a small Nalgene vial containing 200 μl of Ultrapure concentrated nitric acid. A weighed amount of tentacular tissue (50–100 mg) was stored in Nalgene vials with 500 μl of nitric acid. Water samples from each beaker were collected at the end of each experiment and stored in Nalgene vials with 100 μl of nitric acid. When digestion was complete, all samples were diluted with nanopure water and refrigerated until analysis.

Sodium, potassium, calcium, and magnesium were analyzed using flame atomic absorption spectrophotometry. Lanthanum chloride was used to offset anionic interference with calcium and magnesium analyses.

Effect of salinity on osmolality of mesogleal fluid

Medusae were acclimated for 1 wk at salinities of 5‰, 12‰, 15‰, and 20‰. Mesogleal fluid from both bell and tentacles was drawn into calibrated hemocrit tubes and osmotic pressure determined using a Wescor 5500 vapor pressure osmometer. Osmotic pressure was also measured in the corresponding samples of external media. Osmolality in media and mesogleal fluid was expressed per kilogram, based on weight determinations made of both samples.

Size and weight changes in ephyrae and medusae

Ephyrae used for experiments were 2–3 mm in diameter; others, fed on *Artemia* nauplii, were grown to greater sizes for determinations of diameter and weight. A binocular microscope equipped with a micrometer eyepiece was used to measure diameters; a Cahn microbalance was used for weights. Weights of ephyrae used in experiments were estimated from a regression curve relating empirical measurements of diameter and wet weight over a range of animal sizes.

Medusa weights were determined directly by removing animals from the media, rinsing and blotting them lightly to remove surface water and gastrovascular fluid, and transferring them to a plastic weighing tray on a top-pan balance. To estimate the relative contributions of mesogleal fluid and tissue to total medusa weight, eight medusae were weighed as above. Then the bell and tentacles were separated and weighed. The bell and tentacles were next sliced into small pieces, thoroughly blotted with laboratory wipes, and reweighed; this weight was subtracted from the total wet weight to estimate the

mesogleal fluid weight. No correction was made for the fibrous component of the mesoglea, which was included in the tissue weight. Some contamination of the mesogleal fluid component by gastrovascular fluid may have occurred, but most of the latter was removed by the initial blotting. Finally the residue was dried thoroughly and reweighed to obtain a percentage solid material.

During salinity transfer experiments, we observed weight losses that were probably caused by starvation. To better understand the role of starvation in weight loss, a single controlled feeding experiment was conducted using ephyrae fed cultured rotifers (*Brachionis*). The diameters of 24 ephyrae acclimated to a salinity of 20‰ were measured. The animals were placed into individual multi-wells containing 2 ml of 20‰ water. The ephyrae were divided into three feeding groups: unfed, 5 rotifers d^{-1}, and 10 rotifers d^{-1}. At 24 h, the ephyrae were measured, their water was changed, and the appropriate number of rotifers was added to each well. Measurements were repeated at 48 h, and growth was recorded as the mean daily increase in ephyra diameter.

Sulfate in medusa tissue

Weighed tissue samples were dissolved in Ultrapure concentrated nitric acid and diluted with nanopure water. Total sulfate was determined with a Dionex ion chromatograph. Sulfate exchange was measured using $Na_2{}^{35}SO_4$. Small medusae were exposed to radioisotope for periods up to 60 h. The exposure medium had a salinity of 16‰, with $Na_2{}^{35}SO_4$ added to a specific activity of 250 μCi/m*M* SO_4. After isotope exposure the medusae were netted, then triple rinsed, blotted, and weighed. The specific activity of sulfate in the animals was recorded as a percentage of the specific activity of the external medium. ^{35}S was measured with a Packard Tricarb 4000 series liquid scintillation counter.

Statistics

Statistical differences between the mean ionic concentrations of tissue and seawater were tested using *t*-tests with significance determined at the 5% level. Paired *t*-tests were used to evaluate osmolality differences between mesoglea and medium in individual replicates ($P < 0.05$). A line of best bit fit through ^{35}S exchange data was estimated using an iterative (NLIN) hyperbolic regression program (SAS).

Results

Cation concentrations in tissue and mesogleal fluid

Ionic concentrations in tissue and mesogleal fluid generally underwent similar changes when medusae were transferred from a salinity of 20‰ to either 8‰ (experiment 1, Fig. 1) or 12‰ (experiment 2, Fig. 2). Following the transfer of animals from 20‰ to either 8‰ or 12‰, sodium concentrations in tissue and mesogleal fluid were characterized by a rapid drop over the initial 6 h to levels approaching those seen in the external media (Figs. 1A, 2A). Mesogleal sodium also fell, but much slower in the 12‰ medium; at 8‰, the tissue Na concentration made an apparent "recovery" after 1 wk, to a level higher than that of the external medium.

Tissue potassium concentration in animals held at 20‰ was at least twice the corresponding seawater concentration and was generally maintained at levels between 11 and 14 m*M* kg^{-1} over a period of a week in both experiments. However, in experiment 2, tissue potassium in control (20‰) animals rose to a mean level of 17 m*M* kg^{-1}. Tissue potassium levels represented a differential of at least 12 m*M* kg^{-1} compared with the most dilute medium (2 m*M* kg 1^{-1}). In experiment 1 the initial concentration of potassium in mesogleal fluid was significantly higher than at 20‰ ($P < 0.05$). When animals were transferred from 20‰ to 8‰, mesogleal potassium fell to a concentration similar to that of the initial medium (20‰) but significantly higher than the 8‰ medium (Fig. 1B). After a subsequent rise at 24 h it fell again, but remained significantly higher than the 8‰ medium after 1 wk. On transfer from 20‰ to 12‰ (experiment 2), mesogleal potassium concentration showed no significant dilution and remained consistently higher than that of the 12‰ medium over 1 wk. Tissue potassium levels did not change significantly following the transfer of medusae to either 8‰ (Fig. 1B) or 12‰ (Fig. 2B).

In animals transferred from 20‰ to 8‰, concentrations of calcium in both tissue and mesogleal fluid fell after 6 h (Fig. 1C). Thereafter, mesogleal calcium concentration remained significantly higher than concentrations in tissue or in the external medium. Overlap of standard deviations associated with calcium levels of the medium at 20‰ and 12‰ (Fig. 2C) rendered calcium data from experiment 2 equivocal.

Magnesium levels in both salinity transfer experiments showed trends similar to those of calcium. Following transfer of animals from 20‰ to either 8‰ (Fig. 1D) or 12‰ (Fig. 2D), magnesium levels in tissue remained consistently higher than in mesogleal fluid. Both tissue and mesogleal magnesium concentrations remained higher than those of dilute external media for a period of a week.

Transference of medusae from 20‰ to 5‰ caused all animals to fall to the bottom of the experimental beakers. Three out of six medusae began to disintegrate within 36 h; one was unhealthy but alive after 3 days, and two were swimming weakly near the bottom of the beakers. No ionic data were recorded from these animals.

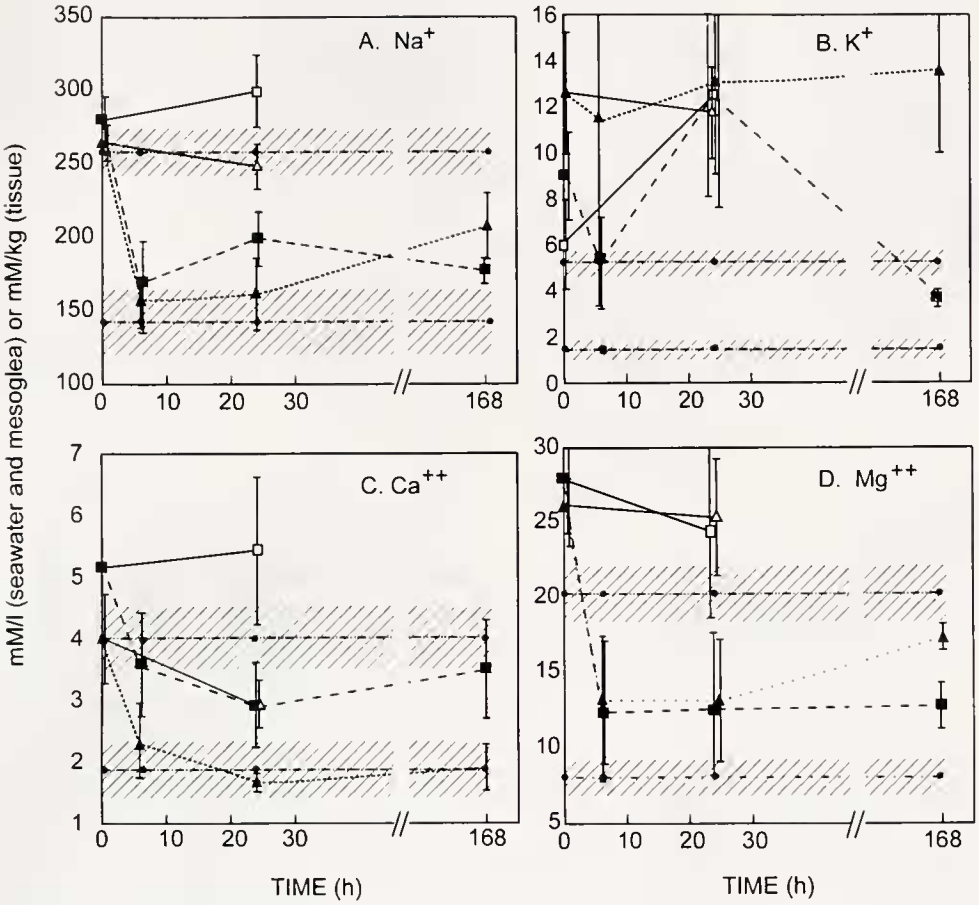

Figure 1. Ion concentrations in mesogleal fluid and tissue of *Chrysaora quinquecirrha* medusae transferred from 20‰ salinity to 8‰. (A) sodium, (B) potassium, (C) calcium, (D) magnesium. Each symbol represents the mean ± 1 SD of six animals. Solid symbols represent ion concentrations in animals transferred from higher to lower salinity at $t = 0$: squares = mesogleal fluid, triangles = tissue. Open squares and triangles represent concentrations in mesogleal fluid and tissue respectively, in animals maintained at 20‰. Dotted horizontal lines represent the mean ionic concentrations of the media in experimental containers (upper = control, lower = treatment) at the end of the experiments; shaded areas represent ±1 SD.

Effect of salinity change on body and tissue weight

All of the foregoing measurements of ionic shifts should be considered against changes in tissue hydration resulting from osmosis. Several experiments were carried out to quantify this phenomenon, although it proved difficult to obtain consistent results. Typical results indicate a wide variation in weight change, even over 24 h (Fig. 3). Changes in salinity from 16‰ to 8‰ resulted in body weight increases between 10% and 15% in whole medusae over 24 h, at which time their body weight was >30% higher than control animals. The time course of the subsequent weight loss was reflected by a concomitant loss in weight of medusae maintained in 16‰ for 1 wk.

Some of this weight loss could have been due to lack of food during the experiments. The diameter of unfed ephyrae in a 48-h controlled feeding experiment was reduced at a daily rate of 2.3% ± 20.5% (SD) (Fig. 4). Ephyra size was positively related to food; diameters increased by 10.6% ± 13.8% d^{-1} in those fed 5 rotifers d^{-1} and by 29.2% ± 25.4% d^{-1} in those fed 10 rotifers d^{-1}.

Osmolality of mesogleal fluid

The osmolality of mesogleal fluid and corresponding seawater was measured in medusae acclimated for 1 wk in 5‰, 12‰, 15‰, and 20‰ (Fig. 5). All animals at 12‰–20‰ exhibited overlap between seawater and mesogleal osmolality, although paired *t*-tests indicated that the osmolality of mesogleal fluid was significantly lower than that of the corresponding external medium at 15‰ and 20‰ ($P < 0.05$). Conversely, animals at 5‰ and 12‰ had significantly higher mesogleal osmolality than that of seawater.

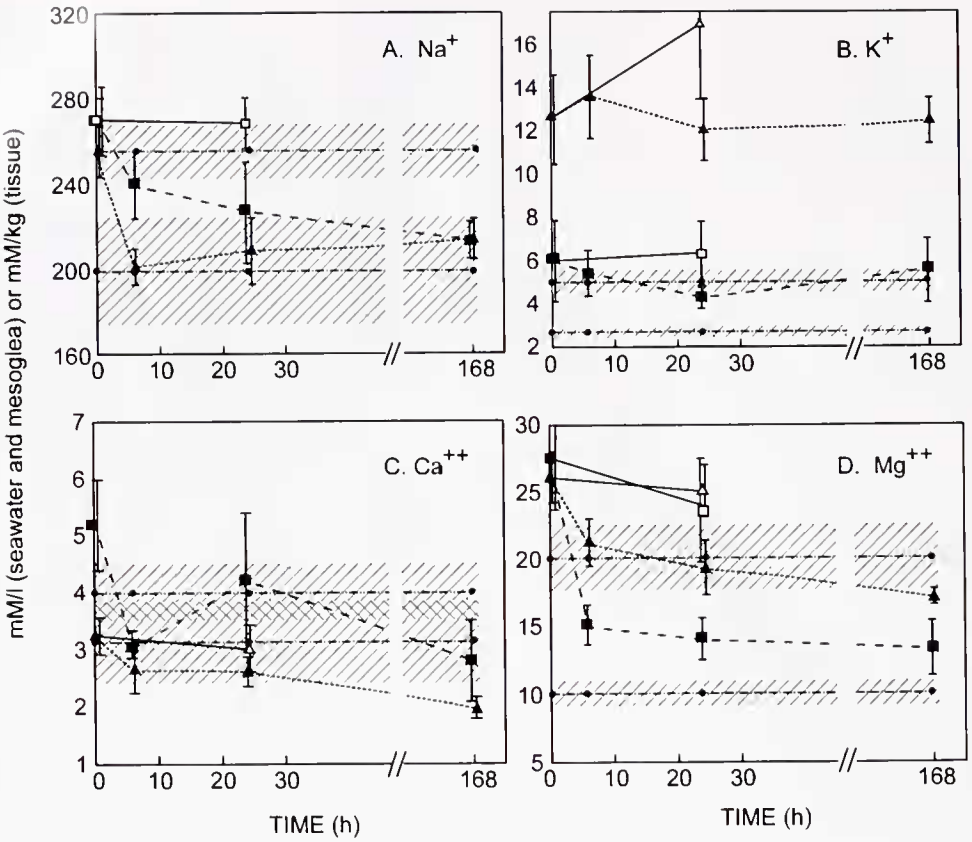

Figure 2. Ion concentrations in mesogleal fluid and tissue of *Chrysaora quinquecirrha* medusae transferred from 20‰ salinity to 12‰. (A) sodium, (B) potassium, (C) calcium, (D) magnesium. Symbols as in Figure 1.

Sulfate

^{35}S exchange at a salinity of 16‰ was complete in about 40 h (Fig. 6) and indicated a freely exchanging component representing about 40% of the total weight. This corresponded closely to the "mesogleal space" of 43% that was estimated from direct measurement of whole medusa, bell, and tentacular tissue weight (Fig. 7). The sulfate concentrations in mesogleal fluid of medusae acclimated [illegible] 20‰, 16‰, and 12‰ are shown in Table I. In [illegible] mesogleal sulfate levels were significantly lower [illegible] the external medium.

Mills (1984) found that [illegible] mesoglea of *Aequorea victoria* hydromedusae maintained [illegible] 24 h at equilibrium in salinities between 23‰ and 38‰ was generally hypoosmolar to the corresponding external medium, although differences between seawater and mesoglea were very small at the lower end of the salinity range. A similar pattern was seen here, although between 15‰ and 12‰ *Chrysaora quinquecirrha* mesoglea switched from being hypo-osmolar to hyperosmolar relative to the external medium. Although there is some overlap in the osmolalities of seawater and mesogleal fluid at salinities between 12‰ and 20‰, paired *t*-tests involving individual replicates reveal significant differences in each case. Nevertheless, differences between mesogleal fluid and seawater remained very small, and *C. quinquecirrha* appeared to be an osmoconformer throughout this range.

Of the ions measured, the most clearly regulated was potassium. Total tissue potassium concentration was approximately 13 mM kg^{-1} and remained stable following transference of medusae from a salinity of 20‰ to 8‰ or 12‰. The apparent rise in tissue potassium in control animals (maintained at 20‰) in experiment 2 (Fig. 2B) was unexplained but did not differ significantly from the corresponding tissue levels in 12‰. The potassium concentration in mesogleal fluid appeared more variable, and values of 8.8 mM kg^{-1} and 6 mM kg^{-1} were recorded at $t = 0$ in experiments 1 and 2. Transference of medusae from 20‰ to 8‰ resulted in fluctuating mesogleal concentrations, including an apparent rise in mesogleal potassium 24 h after the salinity change (Fig. 1B).

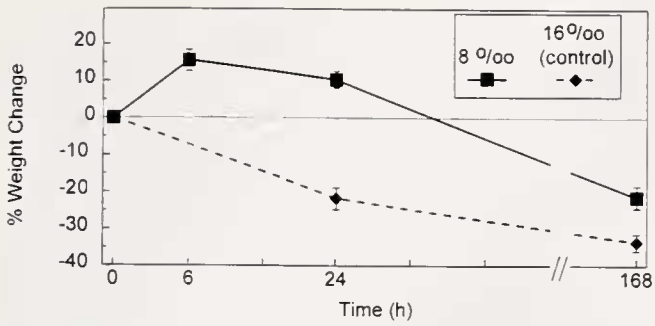

Figure 3. Weight changes in *Chrysaora quinquecirrha* medusae following transfer from 16‰ salinity to 8‰ over 1 week. Means ± 1 SD for eight animals.

This elevation in mesogleal potassium concentration was seen only after the larger salinity change (20‰ to 8‰), and it is possible that osmotic shock may have resulted in a transient increase in cellular potassium permeability or, perhaps, in some cell damage leading to potassium contamination of the mesogleal fluid. A further possibility is that potassium may be actively extruded from cells to mitigate cellular hydration, as has been demonstrated in the freshwater hydromedusa *Craspedacusta sowerbyi* (Fleming and Hazelwood, 1967; Hazelwood *et al.*, 1970). However, in *Craspedacusta*, sodium was also involved (Hazelwood *et al.*, 1970). There is no significant evidence of sodium involvement in volume regulation in *C. quinquecirrha*, and amino acid regulation is probably more important in this regard (Wright, unpubl. data). In the euryhaline sea anemone *Diadumene leucolena*, Pierce and Minasian (1974) demonstrated that volume regulation was achieved through the regulation of the intracellular amino acid pool.

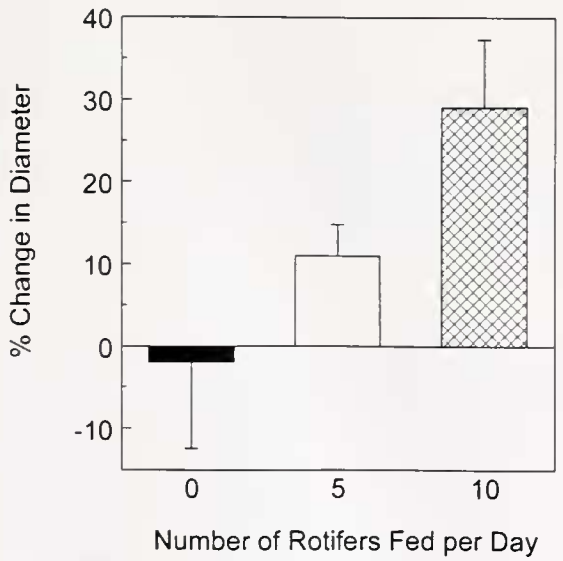

Figure 4. Effect of food ration on size of *Chrysaora quinquecirrha* ephyrae over a 48-h period as determined by measurement of diameter.

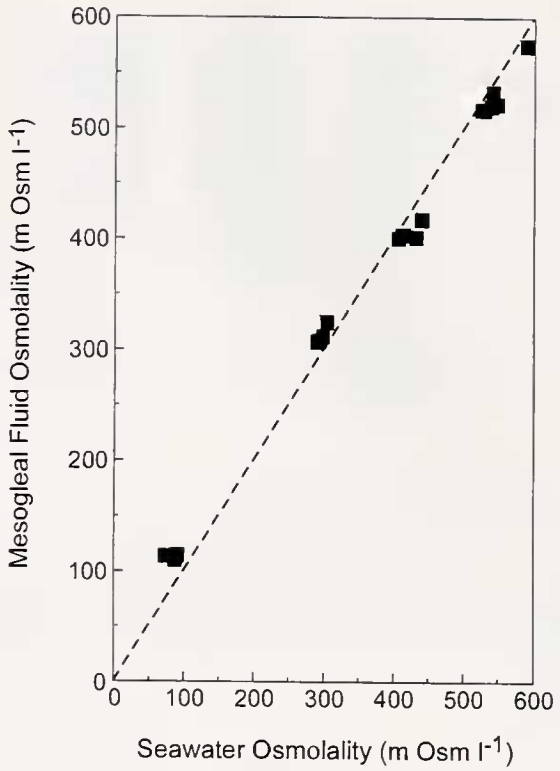

Figure 5. Osmolality of mesogleal fluid and external medium in *Chrysaora quinquecirrha* medusae acclimated for 1 week in salinities of 5‰, 12‰, 15‰, and 20‰. Six individuals were measured at each salinity except for 5‰, where $n = 5$. Some symbols overlay others.

The coincidence of measured sulfate space and our physical determination of extracellular fluid indicated an extracellular space of about 40% in *C. quinquecirrha*. Using this figure and a concentration of 7.4 mM kg^{-1} for mesoglea potassium, one can determine a corrected value for intracellular potassium. The corrected esti-

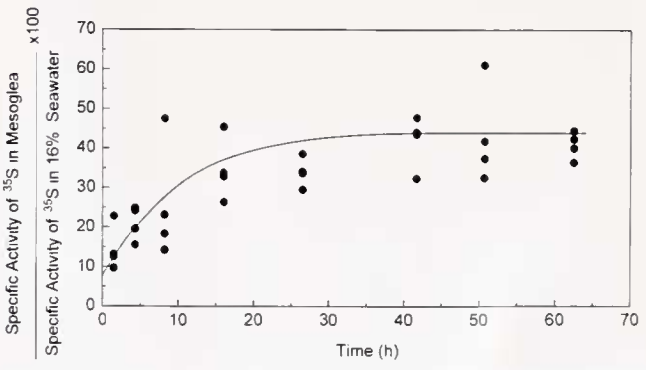

Figure 6. Sulfate exchange in *Chrysaora quinquecirrha* medusae. Exchange was determined as the percentage internal ^{35}S specific activity *versus* external ^{35}S specific activity over 63 h.

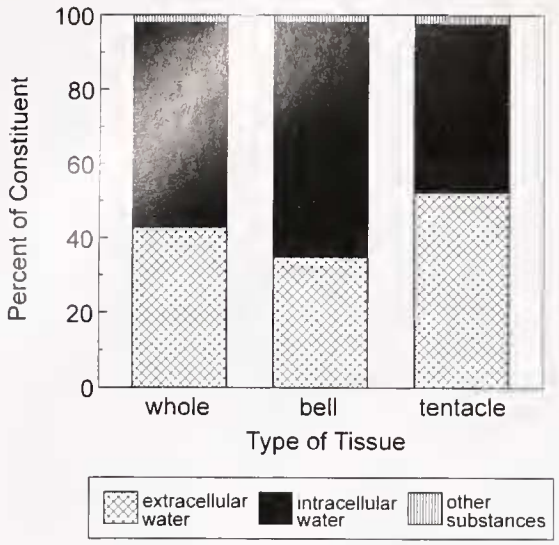

Figure 7. Mesogleal fluid space in bell, tentacles, and whole medusae of *Chrysaora quinquecirrha*. The space, expressed as a percentage of all constituents, was measured directly by weighing the components. "Other substances" refers to dry residue following final drying and reweighing.

mate of 17 mM kg^{-1} calculated in this way is intermediate between the mean values of 10.6 mM kg^{-1} and 29.5 mM kg^{-1} determined by Steinbach (1963) for intracellular potassium in the hydroids *Chlorohydra viridissima* and *Hydra littoralis* in freshwater media. Sulfate space shows considerable variation both within and between species of hydromedusae. Mills and Vogt (1984) reported the sulfate space to be between 10% and 80% in six species of marine hydromedusae. They found that equilibration times varied between <4 h for *Aglantha digitale* and about 85 h for *Mitrocoma cellularia*. The current estimate of 40% sulfate space for *C. quinquecirrha*, with an apparent equilibration time of about 40 h, falls more or less in the middle of this range. At salinities between 20‰ and 12‰, sulfate in the mesogleal fluid of *C. quinquecirrha* is maintained at concentrations lower than those of the external media. Similar results were obtained by Newton and Potts (1993), who reported mesogleal sulfate levels of 40% and 52% of seawater levels in *Cyanea capillata* and *Rhizostoma pulmo* respectively.

In both experiments 1 and 2, there was evidence that the magnesium concentrations in tissue and mesogleal fluid were maintained at levels above that of the external medium. Following transfer of medusae from 20‰ to 12‰, magnesium was substantially diluted in tissue and mesogleal fluid, yet even 7 d after the salinity change, remained significantly higher than the concentration of the dilute medium (Fig. 2D). A similar phenomenon was seen following transfer from 20‰ to 8‰ (Fig. 1D). The concentration of sodium also remained significantly ($P < 0.05$) higher in tissue than in the 8‰ medium.

Dilution resulting from water influx obviously contributed to the fall in tissue ions in most cases. Weight changes in medusae transferred to lower salinities indicated that water influx reached 10%–20% of total body weight within the first 24 h following transfer. But tissue concentrations of sodium, magnesium, and calcium in animals transferred from 20‰ to 8‰ fell by more than 40% in the first 6 h, indicating that diffusional losses of these ions were at least as important as increased tissue hydration in explaining these losses. The apparent subsequent "recovery" of tissue sodium and magnesium to levels above those of the dilute medium suggests that, although these ions may not be actively regulated, the tissue is not freely permeable to them. It is also possible that tissue permeability to these ions changes after the initial osmotic shock. The relative stability of tissue potassium, despite the osmotic swelling, emphasizes the efficiency of the mechanism that regulates cellular potassium in *C. quinquecirrha*.

The degree to which medusae of *C. quinquecirrha* behave like osmometers with changing salinity is difficult to exactly quantify in view of the likely influence of food on weight changes. The controlled feeding experiment illustrated that lack of feeding may account for a weight loss greater than 20% over a 24-h period. This supports the data shown in Fig. 3B. If results from 8‰ animals are corrected for controls (16‰), the 24-h weight change due to osmotic stress may exceed 30%. Medusae of *Aurelia aurita* and *C. quinquecirrha* also decreased in diameter when unfed (Hamner and Jenssen, 1974; Rosen and Purcell, unpubl. data).

In studies conducted here, medusae were able to achieve at least neutral buoyancy in all salinities except one—at 5‰ they remained on the bottom of experimental containers. Bidigare and Biggs (1980) suggested a role for sulfate in adjusting buoyancy in jellyfish. They showed that, by active elimination of more than half of its body SO_4 relative to seawater, the ctenophore *Beroe cucumis* could neutralize its protein mass and achieve neutral buoyancy in dilute seawater. It was postulated that sulfate elimination was offset by isosmotic replacement by chloride. Our data show sulfate concentrations

Table I

Sulfate concentrations in mesogleal fluid of Chrysaora quinquecirrha *medusae adapted to different salinities for 48 h*

Salinity ‰	Seawater sulfate concentration (mM/l)	Mesogleal sulfate concentration (mM/l)	Mesogleal sulfate as percentage seawater
20	13.2	9.1	69
16	9.7	6.8	70
12	7.9	5.2	66

to be consistently lower in tissue of *C. quinquecirrha* than in the external media, but there was no indication of a change in tissue:medium sulfate ratio on transfer of medusae from higher to lower salinity. Therefore, we conclude that *C. quinquecirrha* does not regulate buoyancy by excluding sulfate ions. These medusae are strong swimmers and perhaps would not benefit substantially from ionic buoyancy compensation.

Our results suggest the possibility that medusae of *Chrysaora quinquecirrha* are unable to regulate volume or buoyance at salinities <5‰. This agrees with the distribution of polyps and medusae *in situ* (Cargo and Schultz, 1966, 1967) and with laboratory experiments on asexual reproduction (Purcell *et al.*, unpubl. data).

Acknowledgments

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